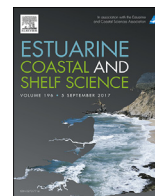




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Epifaunal community composition in five macroalgal species – What are the consequences if some algal species are lost?

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ABSTRACT

Anthropogenic disturbances such as eutrophication and climate change are affecting the distribution and coverage of macroalgae in coastal areas worldwide. How these changes will affect the littoral food webs is challenging to predict as we still lack basic knowledge of epifaunal communities in different macroalgal species. The aim of this study was therefore to compare the epifauna in five common macroalgal species in the northern Baltic Sea. Samples of macroalgae and the associated epifauna were collected in mesh bags at 2 m depth in July–August 2014. The epifaunal abundance data were analyzed with univariate and multivariate methods. The results revealed significant differences in the epifaunal composition among the studied macroalgal species. *Ceramium tenuicorne* hosted the significantly highest and *Fucus vesiculosus* the lowest abundance of epifauna per algal dry weight. When comparing the relative epifaunal abundances in percentage, we found that different epifaunal taxa representing different functional groups dominated *Pylaiella littoralis* (Chironomidae, deposit feeder), *Cladophora rupestris* (*Gammarus* spp., herbivorous/omnivorous) and *Furcellaria lumbricalis* (*Mytilus trossulus*, suspension feeder). However, most of the epifaunal taxa were found in all algal species studied. We conclude that the loss or decline of specific macroalgal species will affect the ecosystem functions and energy flows to the higher trophic levels, but that none of the studied algal species seems to be crucial for the existence of single taxa or functional group of epifauna.

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1. Introduction

Macroalgae are important primary producers along rocky shores worldwide (Ryther, 1963; Mann, 1973; Littler and Murray, 1974) and offer habitats for a variety of marine organisms (Seed and O'Connor, 1981; Norderhaug et al., 2005; Christie et al., 2009). They also contribute to several ecosystem services such as nutrient cycling, CO₂ capture and storage as well as in maintaining the fish stocks by providing nursery and foraging grounds (Costanza et al., 1997; Rönnbäck et al., 2007). The invertebrates living on the algae, epifauna, form an important linkage to higher

trophic levels, as they serve as food for fish (Norderhaug et al., 2005; Eriksson et al., 2009) and birds (MacNeil et al., 1999), as well as affect the host algae by consuming it fresh (Himmelman and Steele, 1971; Jormalainen et al., 2001) or as particulate organic matter (Norderhaug et al., 2003). Grazing may even help to distribute algal spores (Buschmann and Bravo, 1990) and the consumption of diatoms and epiphytic algae from the surface of the host algae enhances the host algae's photosynthesis and growth (Brönmark, 1985; Karez et al., 2000).

A variety of abiotic and biotic factors determine the composition of epifauna associated with macroalgae. Of the macroalgal characteristics, morphological complexity and the available surface area of an alga are often seen as primarily structuring the epifaunal community (Lippert et al., 2001; Parker et al., 2001; Christie et al., 2009; Norderhaug et al., 2014). Nevertheless, macroalgal species also differ in longevity and chemical composition and the associated epifauna differ in their functional characteristics (e.g. Jansson et al., 1982; Steneck and Watling, 1982) such as in size, life cycle and feeding traits. Therefore, it is not surprising that for some epifauna, a specific macroalgal species may offer a better shelter from

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predation (Hacker and Madin, 1991; Svensson et al., 2004; Wernberg et al., 2013) and wave action (Fenwick, 1976; Prathep et al., 2003), better food sources (Orav-Kotta and Kotta, 2003; Poore, 2004; Orav-Kotta et al., 2009), places for larval settlement (Seed et al., 1981) or material for nest building (Brennan and McLachlan, 1979; Råberg and Kautsky, 2007). Indeed, studies worldwide have shown that epifaunal community composition varies between different macroalgal species, but the epifauna are rarely dependent on any single algal species (Taylor and Cole, 1994; Lippert et al., 2001; Parker et al., 2001; Kraufvelin and Salovius, 2004; Bates and DeWreede, 2007).

Information on the relationship between different algal species and associated epifaunal assemblages is needed to predict future changes in the food webs as the macroalgal communities change due to eutrophication (Kangas et al., 1982; Rönnberg et al., 1985; Schramm and Nienhuis, 1996), overfishing of predatory fish (Eriksson et al., 2009; Jackson et al., 2001), changing climate (Harley et al., 2012; Jueterbock et al., 2013; Svensson, 2015) and several other human-induced disturbances such as introduced species (Jormalainen et al., 2016), and trampling and harvesting (Crowe et al., 2000). Furthermore, EU's Marine Strategy Framework Directive requires the member states to address the lack of knowledge of different components of the marine ecosystems such as the macroalgae and benthic invertebrates to be able to develop indicators for measuring potential changes and to protect, preserve and restore the marine environment (European commission, 2008).

In addition to climate change, eutrophication is considered as one of the biggest threats to the macroalgal communities in the Baltic Sea, since it results in shifts in the macroalgal composition from perennial species, such as bladder wrack *Fucus vesiculosus* (L., 1753), to ephemeral fast growing filamentous species such as *Pylaiella littoralis* (L., Kjellman, 1872) (Kangas et al., 1982; Kautsky et al., 1986; Eriksson et al., 1998). Predicted elevated sea water temperatures (Jueterbock et al., 2013) and decreasing salinity (Philippart et al., 2011) due to climate change, will likely decrease the distribution of marine algal species such as fucoids (Jueterbock et al., 2013) and increase the primary production and distribution of filamentous green algae such as *Cladophora glomerata* (L., Kützinger, 1843) (Svensson, 2015). The decline of predatory fish in the Baltic Sea has also been shown to promote bloom forming macroalgae as a result of decreased invertebrate grazer control (Eriksson et al., 2009). These human-induced changes in the macroalgal communities are likely to affect the associated epifauna as well as higher trophic levels (Pihl et al., 1995; Råberg and Kautsky, 2007; Wikström and Kautsky, 2007). Consequently, we need to predict what happens to epifaunal communities if some macroalgal species decline or are even lost from the ecosystem. The decline of *F. vesiculosus* and changes in its epifaunal community are of high concern as *F. vesiculosus* is considered as a key species in the ecosystem hosting a diverse assemblage of epifauna and epiphytes and functioning as a spawning, breeding and foraging ground for fish (Jansson et al., 1982; Kautsky et al., 1992). However, only few studies have compared *F. vesiculosus* associated epifauna to epifauna associated with other macroalgal species (Kraufvelin and Salovius, 2004; Zander et al., 2015). Furthermore, these studies have compared the epifauna of belt forming algal species from different depths and consequently affected by varying exposure to waves, that is known to affect the epifaunal diversity (Norderhaug et al., 2012) as well as secondary production of mobile epifauna (Norderhaug and Christie, 2011). The aim of our study was to compare the epifaunal composition of both ephemeral and perennial, as well as of canopy-forming and filamentous macroalgal species growing side by side at the same depth along the rocky shores. We also discuss the usability of our sampling methodology and how algal species loss may affect the associated epifauna and

higher trophic levels. We hypothesized that the epifaunal community composition would differ among the algal species, as algal species have varying characteristics and may therefore provide different resources for functionally variable epifaunal taxa.

2. Materials and methods

2.1. Study area and the studied macroalgal species

The Baltic Sea is heavily affected by anthropogenic impact (Jutterström et al., 2014), but our study area in the Åland Islands in the northern Baltic (Fig. 1, N 60° E 19°) is one of the most pristine ones since it lacks heavy agriculture and industries, major shipping routes, and large concentrations of people (Nummelin, 2000). The outer archipelago waters are clear allowing light to penetrate deeper than in the inner archipelago, resulting in high algal cover (Krause-Jensen et al., 2009). In these exposed rocky shores, where we conducted our study, annual green filamentous algae can be found most abundantly closest to the surface, canopy-forming brown alga *F. vesiculosus* forms a belt in depths of 2–5 m and red algae are found more abundantly in deeper parts of the shore (Waern, 1952; Kiirikki and Lehvo, 1997; Bäck and Ruuskanen, 2000). Despite the well-known vertical zonation pattern, different macroalgal species are commonly found among the dominant belt forming species (Waern, 1952). We studied five algal species living side by side at 2 m depth along the rocky shores. The algal species studied were *F. vesiculosus*, ephemeral filamentous red alga *Ceramium tenuicorne* (Kützinger, Waern, 1952), ephemeral filamentous brown alga *Pylaiella littoralis*, perennial filamentous green alga *Cladophora rupestris* (L., Kützinger, 1843) and small perennial canopy-forming red alga *Furcellaria lumbricalis* (Dalton, J.V. Lamouroux, 1813) (Fig. 1). In our study area, *F. vesiculosus* was the dominant algal species, but all studied species are commonly found both within and outside the *Fucus* belt and can even build sub-belts of their own (Waern, 1952). *C. tenuicorne* and *P. littoralis* can also grow as epiphytes on *F. vesiculosus* (Waern, 1952).

2.2. Sampling

Sampling was conducted in summer 2014 (July 29 – August 5) when most of the algal species are abundant (Waern, 1952). The sampling was always conducted around the noon (10.00–14.00) to avoid any diurnal variation in the distribution of epifauna (Jørgensen and Christie, 2003). During the sampling period surface water temperature was exceptionally high for the area and fluctuated between 22.4 and 24.2 °C. Salinity was measured using the Practical Salinity Scale and it varied between 5.4 and 5.6. Samples were collected by SCUBA diving and algal specimens were picked by enclosing them in 0.5 mm mesh bags; 50 × 70 cm bag size for large (>30 cm) *F. vesiculosus* samples and 20 × 30 cm bag size for the other smaller (<15 cm) algal species samples. The goal was to get a pure sample of only one algal species; a similar method has also used by e.g. Taylor and Cole (1994), Lippert et al. (2001) and Bates (2009). Between 9 and 14 samples of each algal species were collected, 59 samples in total (for exact number of samples see Fig. 1). Samples were collected randomly by diving along gently sloping coastlines at four different study sites (at a distance of 0.5–4 km from each other) with a similar level of exposure to waves (classified as exposed shores, see Isæus, 2004). However, samples of *F. vesiculosus* and *F. lumbricalis* with high epiphytic algal cover were avoided, as were filamentous algal specimens growing as epiphytes. All samples were collected at 2 m (±25 cm) depth, preserved in 80% ethanol and analyzed under a light microscope (10 X, NIKON SMZ 1500) in the laboratory. After removing the epifauna, the algal samples were dried at 65 °C for 2–3 days until a

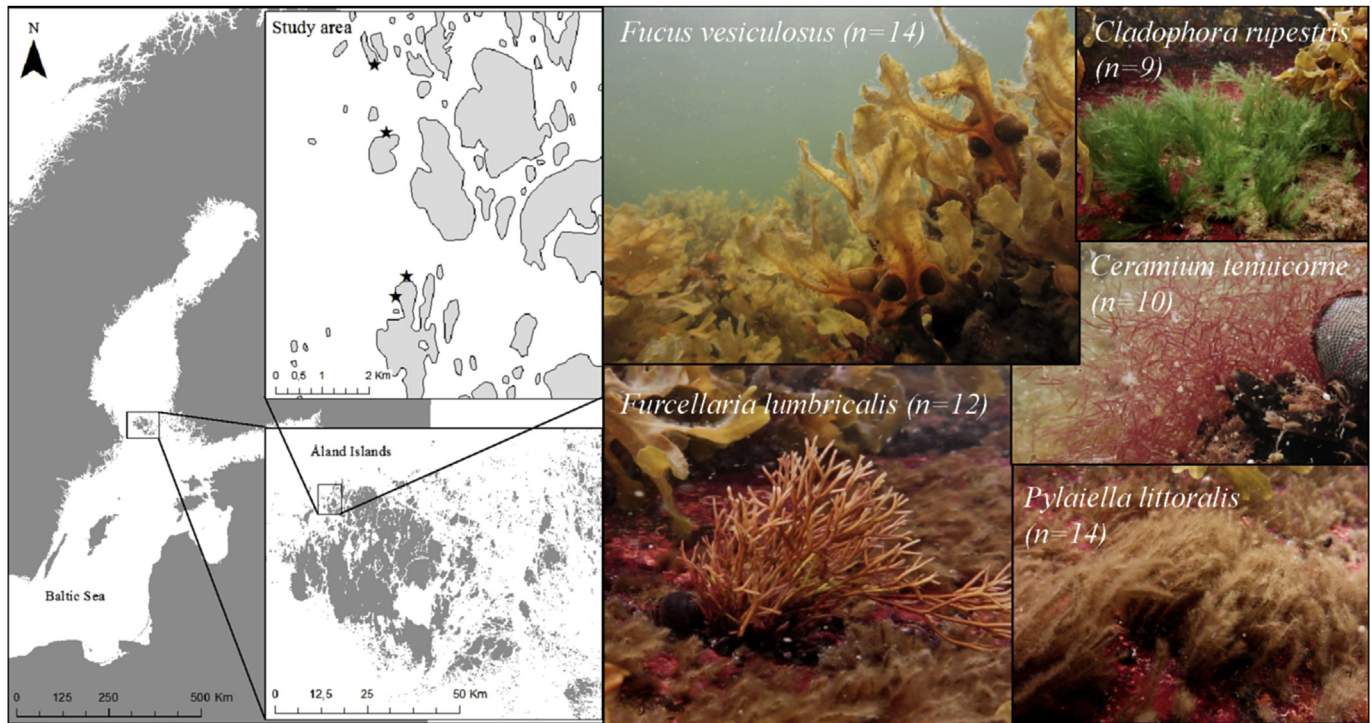


Fig. 1. Map of the location of the study area (stars indicate the individual study sites). To the right; images of the five studied algal species, including the number of samples of each species.

constant dry weight was reached. All macroscopic (>0.5 mm, Duplisea, 2000) epifauna (invertebrates living on the algal surfaces) were counted and determined to lowest taxonomic level possible. Juvenile *Idotea* spp. and *Gammarus* spp. were categorized to respective family level. Insect larvae were often specified only to genus level. Presence of sedentary bryozoan *Electra crustulenta* (Pallas, 1766) was noted but excluded from the abundance analyses as it is hard to measure the number of individuals of the species. The infaunal species *Nereis diversicolor* (Müller, 1776) as well as the nectobenthic species of the order Mysidae were included in the analysis as they were found clearly among the algae. Furthermore, to describe which type of animals utilize different algal species, the 10 most abundant epifaunal taxa of all samples were categorized into functional groups according to feeding types: suspension feeder, deposit feeder, herbivorous/omnivorous and carnivore. Feeding types may vary during different life stages or habitats and therefore we used categorization of the feeding types based on Jansson et al. (1982) and Veber et al. (2009) who also conducted their studies in summer time in the Baltic. The remaining epifaunal taxa were categorized to a group of mixed feeding types.

2.3. Data analysis

The epifaunal abundance data for each sample were first calculated per 1.0 g algal dry weight (hereafter referred to as algal dry weight in the text) by dividing the number of epifauna with the original dry weight of the algal sample. This was done to standardize algal biomass value to 1 g and thus make the samples of different original sizes comparable with each other. To test if all algal species samples could be regarded as independent ones, regardless from which sampling site they were taken, all data were tested for normal distribution (Shapiro-Wilk test, IBM SPSS Statistics 21) where after the homogeneity of variances between the different sampling sites for each algal species was tested (Levene's test, IBM SPSS Statistics 21). All data were normally distributed and

homogeneity of variances was reached (requiring log transformation of the total epifaunal abundance data of *P. littoralis*, *F. lumbricalis* and *F. vesiculosus*). One-way ANOVA with Bonferroni Multiple Comparison Test (GraphPad Prism 5.01) was run to test the differences in the number of epifaunal taxa, total epifaunal abundance and Shannon-Wiener diversity index (H') between the studied algal species. Homogeneity of variances in the total epifaunal abundance and number of epifaunal taxa between the algal species were tested with Bartlett's test for equal variances (GraphPad Prism 5.01). Log transformation was used for the epifaunal abundance data to reach homogeneity of variances between the studied algal species.

Differences in the overall community composition of epifauna among the studied algal species were analyzed with analysis of similarity (one-way ANOSIM, PRIMER 7.0.11). A similarity percentage analysis (SIMPER, PRIMER 7.0.11) was run to assess which of the epifaunal taxa contributed the most to the differences in the epifaunal composition between the algal species. These analyses were run both with epifaunal abundance data calculated for algal dry weight as well as in relative abundances (percent composition of number of epifaunal individuals of different taxa relative to the total number of epifaunal individuals in the sample representing 100%) to allow comparison of the epifaunal dominance structure between the algal species. Data were not transformed to avoid emphasizing rare epifaunal species, as the algal samples originally differed in size, and therefore it was more likely that rare species would be found more frequently in the large *F. vesiculosus* samples than in the other algal species samples. The results, showing also from which sampling site the samples were taken, were visualized with nonmetric multidimensional scaling (nMDS). The Bray Curtis similarity index was used in all multivariate analyses. The 10 most abundant epifaunal taxa of all the samples were chosen for the comparison of functional groups within each algal species and displayed in percentages.

3. Results

3.1. Differences in number of epifaunal taxa and total abundance

In total, 29 epifaunal taxa were found among the different algae (Table 1). There were significant differences in the number of epifaunal taxa among the studied algal species (one-way ANOVA, $R^2 = 0.6885$; $F_{4,54} = 29.84$; $p < 0.0001$, Fig. 2, A). The ranking of host algae in terms of the number of epifaunal taxa was *F. vesiculosus* > *F. lumbricalis* and *C. rupestris* > *P. littoralis* > *C. tenuicorne*. Six epifaunal taxa were found only in *F. vesiculosus* (*Palaemon* spp., Mysidae, Staphylinidae, Ephemeroptera, Thysanoptera and Trichoptera) and one epifaunal taxon (*Macoma balthica* L., 1758) was found only in *C. rupestris*, but each of these taxa was only represented by one individual (Table 1). The differences in the number of epifaunal taxa between *F. vesiculosus* and the other studied algal species were most likely a result of differing sample sizes. The original dry weights of the algal samples were: (*C. tenuicorne* 0.14 (mean) $\pm$ 0.03 g (SE); *P. littoralis*

0.28 $\pm$ 0.02 g; *C. rupestris* 0.30 $\pm$ 0.08; *F. lumbricalis* 1.27 $\pm$ 0.22, *F. vesiculosus* 50.35 $\pm$ 6.95 g). Significant differences were also found in the total epifaunal abundance per algal dry weight between the studied algal species (one-way ANOVA, $R^2 = 0.8355$; $F_{4,54} = 68.56$; $p < 0.0001$, Fig. 2, B) as well as in the Shannon-Wiener diversity index values ($R^2 = 0.4366$; $F_{4,54} = 10.46$; $p < 0.00001$, Fig. 2, C). The ranking of the host algae in terms of epifaunal abundance per algal dry weight was *C. tenuicorne* > *C. rupestris* > *P. littoralis* > *F. lumbricalis* > *F. vesiculosus* and in terms of diversity *F. vesiculosus* > *C. rupestris* > *F. lumbricalis* > *C. tenuicorne* > *P. littoralis*.

3.2. Differences in the epifaunal community composition

In the nMDS ordination based on the epifaunal abundances per algal dry weight, samples of different algal species formed distinct groups. No clear groupings were formed by the sampling sites indicating that the largest differences in epifaunal composition were algal species specific, but not site specific (Fig. 3, A). As an

Table 1

Mean and standard error ($\pm$ SE) of the abundances of the epifaunal taxa in the studied macroalgal species. The epifaunal abundances are calculated per g algal dry weight. Total number of epifaunal taxa and Shannon-Wiener diversity index value for each algal species is also given in the bottom of the table.

Taxonomic group	<i>Ceramium tenuicorne</i> (Kützing, Waern, 1952)		<i>Pyraliella littoralis</i> (L., Kjellman, 1872)		<i>Cladophora rupestris</i> (L., Kützing, 1843)		<i>Furcellaria lumbricalis</i> (Hudson, J.V.Lamouroux, 1813)		<i>Fucus vesiculosus</i> (L., 1753)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
MOLLUSCA										
<i>Mytilus trossulus</i> (Gould, 1850)	165	58	6	2	18	6	56	13	3	1
<i>Theodoxus fluviatilis</i> (L., 1758)	56	9	6	5	8	3	8	1	3	<1
Hydrobiidae	118	38	46	12	8	3	8	2	2	1
Cerastoderma spp.	27	17	21	6	22	7	2	1	2	1
<i>Lymnaea</i> spp.	0	0	3	2	3	2	0	0	<1	<1
<i>Limapontia capitata</i> (Müller, 1773–1774)	0	0	0	0	9	5	0	0	<1	<1
<i>Macoma balthica</i> (L., 1758)	0	0	0	0	<1	<1	0	0	0	0
ARTHROPODA										
<i>Idotea</i> spp.	80	26	4	1	34	8	20	8	2	1
<i>Jaera</i> spp.	140	32	1	<1	42	23	18	7	3	<1
<i>Gammarus</i> spp.	90	22	8	4	99	23	7	1	3	1
Chironomidae	65	18	87	22	36	8	3	1	3	<1
Ostracoda	35	20	10	4	8	4	8	3	1	<1
Halacaridae	9	5	5	2	27	12	8	2	<1	<1
Copepoda	1	1	<1	<1	4	2	<1	<1	<1	<1
<i>Palaemon</i> spp.	0	0	0	0	0	0	0	0	<1	<1
Mysidae	0	0	0	0	0	0	0	0	<1	<1
<i>Balanus improvisus</i> (Darwin, 1854)	0	0	0	0	0	0	<1	<1	<1	<1
Staphylinidae	0	0	0	0	0	0	0	0	<1	<1
Ephemeroptera	0	0	0	0	0	0	0	0	<1	<1
Thysanoptera	0	0	0	0	0	0	0	0	<1	<1
Trichoptera	0	0	0	0	0	0	0	0	<1	<1
ANNELIDA										
Oligochaeta	8	7	18	7	20	8	3	1	<1	0
<i>Nereis diversicolor</i> (Müller, 1776)	0	0	0	0	0	0	<1	<1	<1	<1
<i>Pisiccola geometra</i> (L., 1761)	0	0	0	0	0	0	<1	<1	<1	<1
NEMATODA										
	0	0	5	2	4	2	<1	<1	<1	<1
PLATYHELMINTHES										
Turbellaria	0	0	3	1	1	1	3	1	<1	<1
PRIAPULIDA										
<i>Halicryptus spinolosus</i> (Von Siebold, 1849)	3	3	0	0	<1	<1	1	<1	<1	<1
NEMERTEA										
<i>Cyanophthalma obscura</i> (Schultze, 1851)	0	0	4	2	<1	<1	1	1	<1	<1
BRYOZOA										
<i>Electra crustulenta</i> (Pallas, 1766)							x		x	
Total abundance (mean & SE)	798	98	228	34	345	67	149	26	23	2
Total number of taxa	13	–	16	–	19	–	20	–	28	–
Mean of Shannon-Wiener diversity (H')	1.7	0.06	1.6	0.07	2.0	0.11	1.9	0.06	2.1	0.04

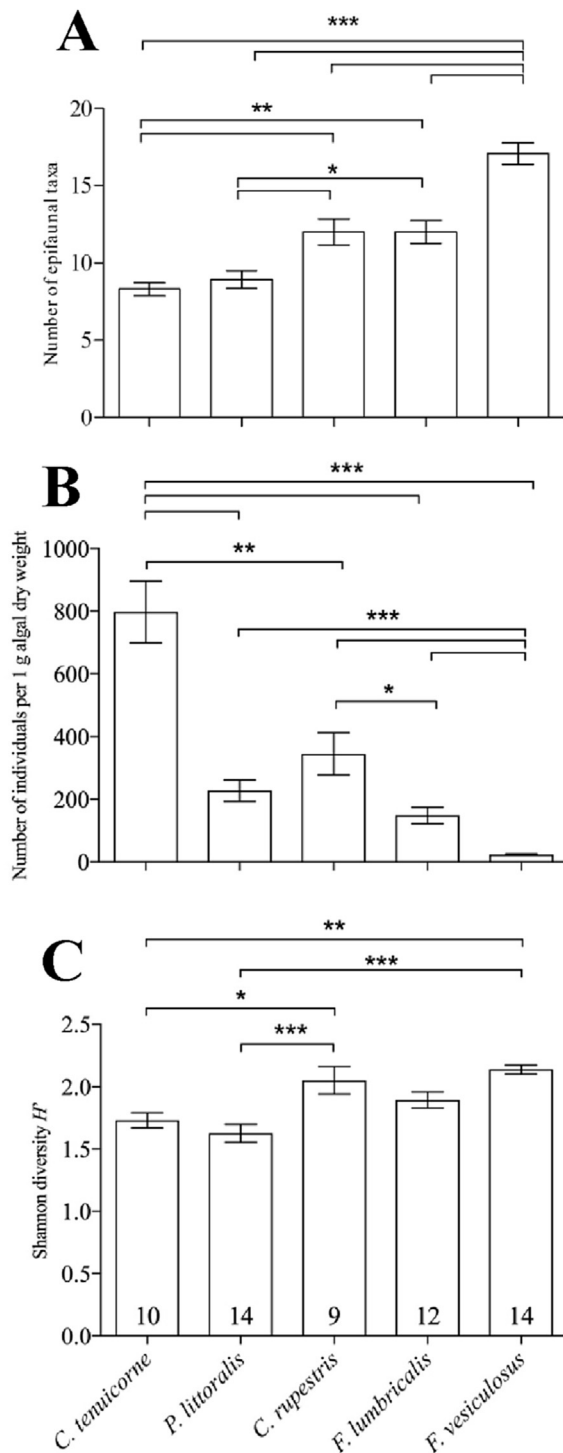


Fig. 2. Comparison of (A) number of epifaunal taxa and (B) number of individuals of epifauna per g algal dry weight and (C) Shannon-Wiener diversity values (H') between the studied macroalgal species. Figures display mean value and SE. The number in each bar in plate C, indicate the number of samples of each algal species. The horizontal lines connect statistically different species and asterisks indicate degree of significance level determined by one-way ANOVA tests and Bonferroni post doc tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

exception, epifaunal communities in *C. rupestris* overlapped partly with the epifaunal communities in other algal species samples. A similar pattern was found in the nMDS ordination that was based on the relative epifaunal abundances in percentage, but in this

ordination, epifaunal communities in *C. tenuicorne* and *C. rupestris* overlapped partly with epifaunal communities in the other algal species (Fig. 3, B). The one-way ANOSIM analysis (Table 2) showed significantly differentiating epifaunal composition between the macroalgal species both per algal dry weight (Global R: 0.843, $p < 0.1\%$) and in relative epifaunal abundances in percentage (Global R: 0.606, $p < 0.1\%$).

The epifaunal abundance per algal dry weight was significantly lower in *F. vesiculosus* than in other algal species resulting in significant differences in the epifaunal composition (one-way pairwise comparison ANOSIM, Table 2, A, SIMPER, Table 3, A). Also, the epifaunal composition in the other algal species differed significantly from each other (one-way pairwise comparison ANOSIM, Table 2, A), mainly as a result of *C. tenuicorne* hosting a higher number of *Jaera* spp., *M. trossulus* and Hydrobiidae, and *P. littoralis* and *C. rupestris* hosting more Chironomidae and Gammarus spp., respectively, than the other algal species (SIMPER, Table 3, A). When the relative epifaunal abundances (%) were compared, the largest differences were found between *F. lumbricalis* and *P. littoralis* and between *F. lumbricalis* and *C. rupestris* (one-way ANOSIM pairwise comparison, R: 0.915 respective 0.888, Table 2, B), whereas the epifaunal composition between *C. tenuicorne* and *F. vesiculosus* and between *C. tenuicorne* and *F. lumbricalis* did not differ as clearly (one-way ANOSIM pairwise comparison, R: 0.332 and 0.296 Table 2, B). The SIMPER analysis revealed differences in dominant epifaunal taxa (SIMPER, Table 3, B) representing different functional groups: deposit feeders in filamentous brown alga *P. littoralis*, suspension feeders (*M. trossulus*) in the canopy-forming red alga *F. lumbricalis* and herbivorous/omnivorous gammarids in the filamentous green alga *C. rupestris*. The red filamentous alga *C. tenuicorne* had a slight dominance of suspension feeders (*M. trossulus*) and herbivorous/omnivorous isopod *Jaera* spp., but also other epifaunal taxa were well represented. The big canopy-forming brown alga *F. vesiculosus* hosted a more even epifaunal composition (Fig. 4).

4. Discussion

4.1. Main results

As macroalgal communities are changing due to several anthropogenic disturbances (Schramm and Nienhuis, 1996; Jackson et al., 2001; Harley et al., 2012), it is crucial to understand the importance of different algal species for the epifauna and further for the littoral food webs. Our results show that there are clear differences in the epifaunal composition between the studied algal species but only few if any epifaunal taxa are dependent on any single algal species, which is also supported by results from earlier studies (Taylor and Cole, 1994; Lippert et al., 2001; Kraufvelin and Salovius, 2004; Bates and DeWreede, 2007). The Shannon-Wiener diversity index shows that both *F. vesiculosus* and *C. rupestris* have statistically higher diversity of epifauna compared to the annual filamentous algae *P. littoralis* and *C. tenuicorne*.

4.2. Differences in the epifaunal community composition

The distribution of epifauna appears to be dependent on the functional characteristics of both algal and epifaunal species, as the total epifaunal abundance differed among the studied algal species even though they were collected from same depth and same sampling sites with similar exposure to waves. Further, there were differences in the dominant epifaunal taxa and epifaunal functional groups among the studied algal species. *C. tenuicorne* hosted the significantly highest abundance of epifauna, which partly could be explained by the filament structure of *C. tenuicorne* that provides

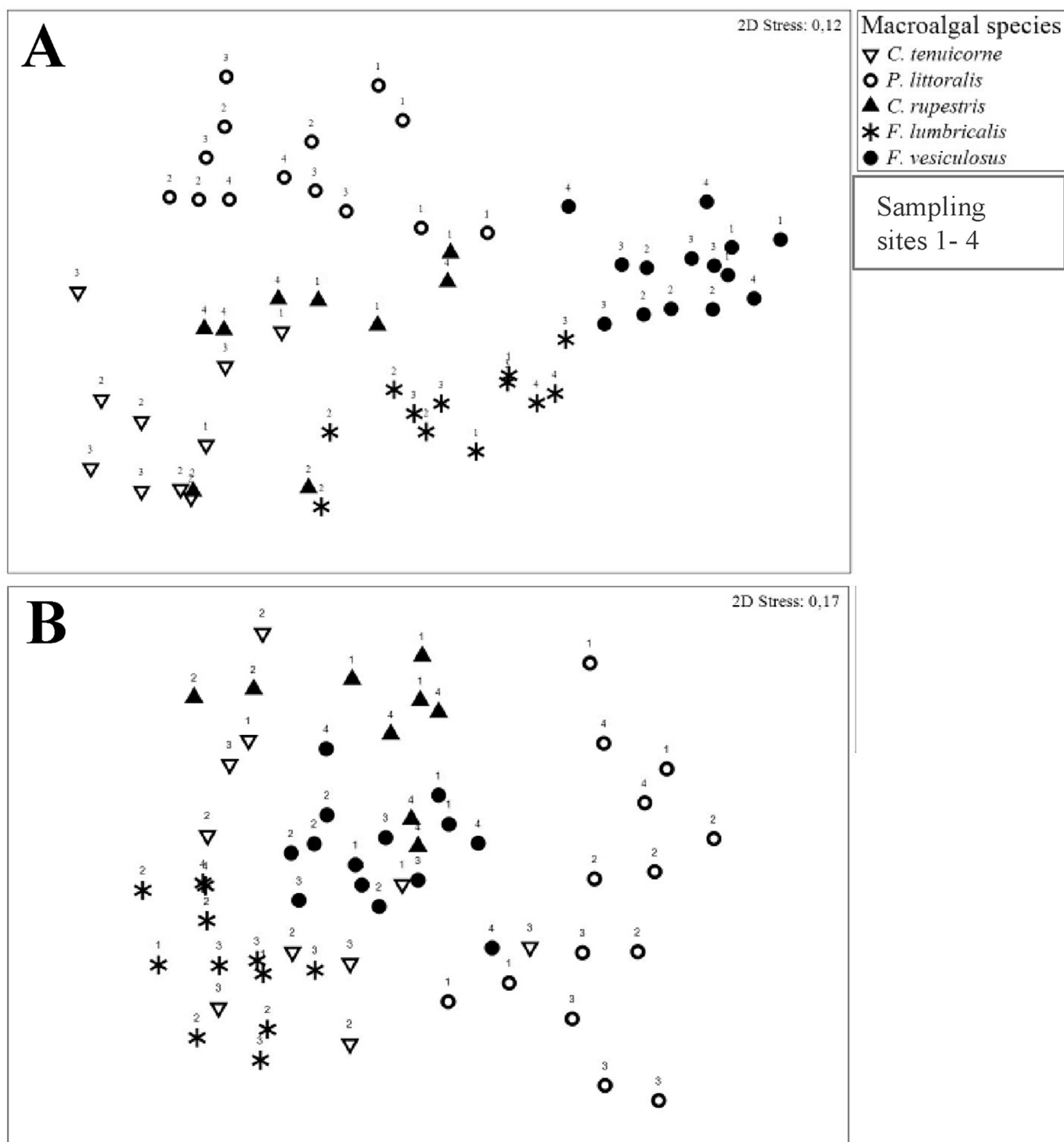


Fig. 3. nMDS ordination of the different algal species samples according to their epifaunal composition, (A) epifaunal abundances per g algal dry weight and (B) relative epifaunal abundances in %. Numbers 1–4 stand for the sampling sites.

large surface area and therefore increased living space for small sized epifauna (Morse et al., 1985). The filament structure may also increase protection from predation and wave action (Hacker and Steneck, 1990; Davenport et al., 1999). Nevertheless, *C. tenuicorne* hosted also significantly higher abundance of epifaunal individuals compared to the other two filamentous algal species, and therefore it is unlikely that only the structure of the algae would determine the epifaunal composition in this algal species. The chemical

composition of the *C. tenuicorne* during the time of sampling could be another reason for the high epifaunal abundances. In contrast to the other studied algal species, *C. tenuicorne* was in a late successional stage, being still attached, but not completely fresh. The decomposing stage may have attracted herbivores as many of the algae's chemical defense substances start to break down as the algae age (Little et al., 2009). The high numbers of blue mussel *M. trossulus* in *C. tenuicorne*, also noted by Wallin et al. (2011) and

Table 2
One-Way ANOSIM results showing (A) global R, significance level and pairwise comparison between the different macroalgal species according to their epifaunal composition (epifaunal abundances calculated per g algal dry weight) and (B) global R, significance level and pairwise comparison between the different macroalgal species according to their epifaunal composition (relative abundances in %).

Differences in the epifaunal community composition between macroalgal species groups (One-Way ANOSIM)									
Epifaunal composition calculated per 1.0 g algal dry weight					Epifaunal composition in relative abundances (%)				
Global R: 0.843 Significance level of sample statistic: 0.1%					Global R: 0.606 Significance level of sample statistic: 0.1%				
A					B				
Pairwise comparison	R	Significance	Actual	Number >=	Pairwise comparison	R	Significance	Actual	Number >=
Groups	Statistic	Level %	Permutations	Observed	Groups	Statistic	Level %	Permutations	Observed
<i>C. tenuicorne</i> , <i>F. vesiculosus</i>	1	0.1	999	0	<i>C. tenuicorne</i> , <i>F. vesiculosus</i>	0.332	0.1	999	0
<i>C. tenuicorne</i> , <i>F. lumbricalis</i>	0.854	0.1	999	0	<i>C. tenuicorne</i> , <i>F. lumbricalis</i>	0.296	0.1	999	0
<i>C. tenuicorne</i> , <i>P. littoralis</i>	0.774	0.1	999	0	<i>C. tenuicorne</i> , <i>P. littoralis</i>	0.661	0.1	999	0
<i>C. tenuicorne</i> , <i>C. rupestris</i>	0.555	0.1	999	0	<i>C. tenuicorne</i> , <i>C. rupestris</i>	0.522	0.1	999	0
<i>F. vesiculosus</i> , <i>F. lumbricalis</i>	0.891	0.1	999	0	<i>F. vesiculosus</i> , <i>F. lumbricalis</i>	0.704	0.1	999	0
<i>F. vesiculosus</i> , <i>P. littoralis</i>	0.958	0.1	999	0	<i>F. vesiculosus</i> , <i>P. littoralis</i>	0.709	0.1	999	0
<i>F. vesiculosus</i> , <i>C. rupestris</i>	0.972	0.1	999	0	<i>F. vesiculosus</i> , <i>C. rupestris</i>	0.613	0.1	999	0
<i>F. lumbricalis</i> , <i>P. littoralis</i>	0.835	0.1	999	0	<i>F. lumbricalis</i> , <i>P. littoralis</i>	0.915	0.1	999	0
<i>F. lumbricalis</i> , <i>C. rupestris</i>	0.726	0.1	999	0	<i>F. lumbricalis</i> , <i>C. rupestris</i>	0.888	0.1	999	0
<i>P. littoralis</i> , <i>C. rupestris</i>	0.519	0.1	999	0	<i>P. littoralis</i> , <i>C. rupestris</i>	0.7	0.1	999	0

Eriksson Wiklund et al. (2012), may be a result of blue mussel larvae settling preferentially on this particular algal species (Bayne, 1964).

The reason for *P. littoralis* hosting many deposit feeders (Chironomids and Hydrobidae) may be linked to the very fine structure of *P. littoralis* filaments, which trap particles and sediment. Organic matter in sediment is preferred by deposit feeders as food and together with sediment even as nest building material (Prathep et al., 2003), whereas the accumulating sediment may affect negatively other epifaunal species such as the suspension feeder *M. trossulus* (Westerbom et al., 2008) that was rare in *P. littoralis*. Chironomids living in *P. littoralis* were also often found inside tubes made out of *P. littoralis*, further giving camouflage and protection from predators. Surprisingly, herbivorous/omnivorous isopods and gammarids were few in *P. littoralis* even though they have been shown to prefer this algal species as food (Kotta et al., 2000; Orav-Kotta and Kotta, 2003; Orav-Kotta et al., 2009). Mobile epifauna, such as isopods and gammarids, are known to be more active during night and therefore possibly less susceptible to predation by fish in the darkness (Martin-Smith, 1993; Jørgensen and Christie, 2003). The diurnal variation for these mobile taxa is not clear and it is possible that some algae are used as food during night and others as suitable habitats during daytime as suggested by Buschmann (1990).

In our study gammarids were the dominant epifauna in the filamentous green alga *C. rupestris*. Gammarids are also abundant in other green filamentous algae such as *C. glomerata* (Jansson, 1967; Salovius and Kraufvelin, 2004), *Acrosiphonia* aff. *flagellata* (Kjellman, 1893) (Lippert et al., 2001) and *Enteromorpha* sp. (Zander et al., 2015), suggesting that gammarids may prefer green filamentous algae as habitats. There are also examples of amphipods choosing habitats of higher structural complexity (Hansen et al., 2011) and habitats where their bodies become cryptic (Keith, 1971; Hacker and Steneck, 1990) and in our study *C. rupestris* also provided good protection and camouflage for the gammarids. *C. rupestris* hosted also the second highest epifaunal diversity of all the studied algal species.

The canopy-forming red alga *F. lumbricalis* was dominated by the suspension feeder *M. trossulus*, and similar results have also been reported by Bučas (2009) and Westerbom et al. (2008). The alga is perennial and has a strong structure that provides a habitat where the *M. trossulus* larvae can settle and grow relatively large before moving on to the bare bottom. In addition, the alga may provide good feeding conditions for *M. trossulus* (Westerbom et al.,

2008).

In the other canopy-forming species *F. vesiculosus*, the epifaunal community structure was more even. The epifaunal taxa present were found in similar abundances, suggesting that *F. vesiculosus* hosts a diverse (highest epifaunal diversity of all the studied algal species) epifaunal assemblage but is not particularly important for any specific taxa, as also suggested by Wikström and Kautsky (2007). As an exception, the sessile species *E. crustulenta* and *Balanus improvisus* (Darwin, 1854) were found only in the canopy-forming species *F. vesiculosus* and *F. lumbricalis*. Nevertheless, both *E. crustulenta* and *B. improvisus* are abundantly found on bare hard surfaces (Grzelak and Kuklinski, 2010) and therefore their dependence on the algae as habitat is questionable. The large mass of *F. vesiculosus* (50–500 × higher dry weight than the weight of the other studied algal species) was most likely the reason for *F. vesiculosus* hosting the highest number of epifaunal taxa and six epifaunal taxa that were not found in any of the other algal species studied. Each of the six epifaunal taxa was only presented by one individual and many of these epifaunal taxa have also been found in filamentous algae in earlier studies (Kraufvelin and Salovius, 2004; Wikström and Kautsky, 2007) and therefore it is unlikely that these epifaunal taxa would be specifically dependent on *F. vesiculosus*. The lowest abundance of epifauna in *F. vesiculosus* compared to the other studied algal species is likely due to the algal structure that does not provide as large surface area per dry weight as the other studied algal species do or may even be a result of higher predation success of fish in *F. vesiculosus* compared with the predation among the dense filamentous algal structures (Holmlund et al., 1990; Pihl et al., 1995).

4.3. Reef wide impacts of algal species loss

Kraufvelin and Salovius (2004) found that in the northern Baltic Sea epifaunal abundances per area were clearly higher in the filamentous algae *C. glomerata* (5000–90,000 individuals/m²) than in *F. vesiculosus* (1000–16,000 individuals/m²). If we assume that the filamentous algae *C. tenuicorne* and *F. vesiculosus* in our study would account for similar dry weight per m² as these species did (70 respective 210 g algal DW/m²) in Kraufvelin and Salovius (2004), the total faunal abundance would be 22,000–85,000 individuals/m² for *C. tenuicorne* and only 2310–8610 individuals/m² for *F. vesiculosus*. In the Gulf of Riga, the Baltic Sea, *F. vesiculosus*, *C. tenuicorne*, *P. littoralis* and *F. lumbricalis* have occurred with

Table 3

SIMPER results showing the epifaunal taxa contributing the most (average abundance and cumulative contribution in %) to the differences in the epifaunal composition between the studied algal species. (A) per g algal dry weight and (B) in relative epifaunal abundances in %.

A				B			
Epifaunal abundances in 1.0 g algal dry weight				Relative epifaunal abundances (%)			
Groups <i>C. tenuicorne</i> & <i>F. vesiculosus</i>		Average dissimilarity = 94.65		Groups <i>C. tenuicorne</i> & <i>F. vesiculosus</i>		Average dissimilarity = 47.14	
Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>F. vesiculosus</i> Av.Abund	Cum.%	Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>F. vesiculosus</i> Av.Abund	Cum.%
<i>Jaera</i> spp.	139.81	2.8	20.23	<i>Jaera</i> spp.	20.14	13.12	15.4
<i>M. trossulus</i>	164.89	2.54	38.35	<i>M. trossulus</i>	18.02	9.64	29.67
Hydrobidae	118.11	2.32	52.01	Hydrobidae	13.51	8.61	41
<i>Gammarus</i> spp.	89.96	2.83	63.69	<i>Idotea</i> spp.	10.07	7.88	50.84
Groups <i>C. tenuicorne</i> & <i>F. lumbricalis</i>		Average dissimilarity = 77.63		Groups <i>C. tenuicorne</i> & <i>F. lumbricalis</i>		Average dissimilarity = 50.84	
Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>F. lumbricalis</i> Av.Abund	Cum.%	Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>F. lumbricalis</i> Av.Abund	Cum.%
<i>Jaera</i> spp.	139.81	17.66	19.68	<i>M. trossulus</i>	18.02	36.11	21.85
<i>M. trossulus</i>	164.89	56.31	35.82	<i>Jaera</i> spp.	20.14	11.89	36.88
Hydrobidae	118.11	7.63	49.94	Hydrobidae	13.51	5.91	47.98
Groups <i>F. vesiculosus</i> & <i>F. lumbricalis</i>		Average dissimilarity = 74.11		Groups <i>F. vesiculosus</i> & <i>F. lumbricalis</i>		Average dissimilarity = 52.33	
Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>F. lumbricalis</i> Av.Abund	Cum.%	Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>F. lumbricalis</i> Av.Abund	Cum.%
<i>M. trossulus</i>	2.54	56.31	38.73	<i>M. trossulus</i>	9.64	36.11	25.51
<i>Idotea</i> spp.	1.78	20.37	50.28	Chironomidae	13.7	3.31	35.63
<i>Jaera</i> spp.	2.8	17.66	60.99	<i>T. fluviatilis</i>	15.77	6.65	45.01
Groups <i>C. tenuicorne</i> & <i>P. littoralis</i>		Average dissimilarity = 78.01		Groups <i>C. tenuicorne</i> & <i>P. littoralis</i>		Average dissimilarity = 68.78	
Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%	Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%
<i>Jaera</i> spp.	139.81	0.71	19.37	Chironomidae	9.49	35.67	19.2
<i>M. trossulus</i>	164.89	5.69	36.84	<i>Jaera</i> spp.	20.14	0.35	33.64
Hydrobidae	118.11	45.72	49.2	Hydrobidae	13.51	20.03	45.3
Groups <i>F. vesiculosus</i> & <i>P. littoralis</i>		Average dissimilarity = 86.42		Groups <i>F. vesiculosus</i> & <i>P. littoralis</i>		Average dissimilarity = 61.32	
Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%	Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%
Chironomidae	3.4	87.44	34.91	Chironomidae	13.7	35.67	18.27
Hydrobidae	2.32	45.72	54.59	Hydrobidae	8.61	20.03	30.48
<i>Cerastoderma</i> spp.	2.31	20.64	63.25	<i>T. fluviatilis</i>	15.77	2.62	41.54
Oligochaeta	0.37	18.33	71.91	<i>Jaera</i> spp.	13.12	0.35	51.96
Groups <i>F. lumbricalis</i> & <i>P. littoralis</i>		Average dissimilarity = 78.85		Groups <i>F. lumbricalis</i> & <i>P. littoralis</i>		Average dissimilarity = 75.68	
Faunal groups	Group <i>F. lumbricalis</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%	Faunal groups	Group <i>F. lumbricalis</i> Av.Abund	Group <i>P. littoralis</i> Av.Abund	Cum.%
Chironomidae	5.59	87.44	25.82	<i>M. trossulus</i>	36.11	3.85	21.44
<i>M. trossulus</i>	56.31	5.69	42.85	Chironomidae	3.31	35.67	42.82
Hydrobidae	7.63	45.72	56.4	Hydrobidae	5.91	20.03	53.64
<i>Cerastoderma</i> spp.	2.34	20.64	62.78	<i>Jaera</i> spp.	11.89	0.35	61.31
Groups <i>C. tenuicorne</i> & <i>C. rupestris</i>		Average dissimilarity = 67.75		Groups <i>C. tenuicorne</i> & <i>C. rupestris</i>		Average dissimilarity = 57.32	
Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%	Faunal groups	Group <i>C. tenuicorne</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%
<i>Jaera</i> spp.	139.81	42.47	17.98	<i>Gammarus</i> spp.	11.85	29.54	17.22
<i>M. trossulus</i>	164.89	18.2	35.31	<i>Jaera</i> spp.	20.14	9.11	32.07
Hydrobidae	118.11	7.7	49.05	<i>M. trossulus</i>	18.02	5.48	44.45
<i>Gammarus</i> spp.	89.96	99.01	59.48	Hydrobidae	13.51	2.9	54.98
Groups <i>F. vesiculosus</i> & <i>C. rupestris</i>		Average dissimilarity = 85.34		Groups <i>F. vesiculosus</i> & <i>C. rupestris</i>		Average dissimilarity = 49.39	
Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%	Faunal groups	Group <i>F. vesiculosus</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%
<i>Gammarus</i> spp.	2.83	99.01	30.32	<i>Gammarus</i> spp.	12.31	29.54	18.66
Chironomidae	3.4	35.68	40.64	<i>T. fluviatilis</i>	15.77	2.92	31.7
<i>Idotea</i> spp.	1.78	34.27	50.93	<i>Jaera</i> spp.	13.12	9.11	41.89
<i>Jaera</i> spp.	2.8	42.47	60.03	<i>Cerastoderma</i> spp.	10.51	6.51	49.91
Groups <i>F. lumbricalis</i> & <i>C. rupestris</i>		Average dissimilarity = 69.51		Groups <i>F. lumbricalis</i> & <i>C. rupestris</i>		Average dissimilarity = 60.63	
Faunal groups	Group <i>F. lumbricalis</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%	Faunal groups	Group <i>F. lumbricalis</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%
<i>Gammarus</i> spp.	6.71	99.01	25.76	<i>M. trossulus</i>	36.11	5.48	25.26
<i>M. trossulus</i>	56.31	18.2	39.78	<i>Gammarus</i> spp.	6.19	29.54	44.72
<i>Jaera</i> spp.	17.66	42.47	49.48	<i>Jaera</i> spp.	11.89	9.11	52.67

(continued on next page)

Table 3 (continued)

A				B			
Epifaunal abundances in 1.0 g algal dry weight				Relative epifaunal abundances (%)			
Groups <i>P. littoralis</i> & <i>C. rupestris</i>		Average dissimilarity = 70.11		Groups <i>P. littoralis</i> & <i>C. rupestris</i>		Average dissimilarity = 65.95	
Faunal groups	Group <i>P. littoralis</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%	Faunal groups	Group <i>P. littoralis</i> Av.Abund	Group <i>C. rupestris</i> Av.Abund	Cum.%
<i>Gammarus</i> spp.	8.46	99.01	22.16	<i>Gammarus</i> spp.	4.46	29.54	19.46
Chironomidae	87.44	35.68	38.16	Chironomidae	35.67	10.93	38.23
Hydrobidae	45.72	7.7	49.07	Hydrobidae	20.03	2.9	51.74

biomasses on 40–2000, 5–800, 5–70 respective 10–400 g algal DW/m² (Kautsky et al., 1999; Kotta et al., 2000). When applying the epifaunal densities from our study on these algal biomasses the epifaunal densities would be approximately 432–82,700 (in *F. vesiculosus*), 1605–975,200 (in *C. tenuicorne*), 327–31,800 (in *P. littoralis*) respective 529–131,700 (in *F. lumbricalis*) individuals/m². These theoretical calculations also indicate that the filamentous algae may have a much more important role in sustaining secondary production than the canopy building species. Furthermore, filamentous algae *C. tenuicorne*, *P. littoralis* and *C. rupestris* hosted especially isopods, amphipods and insect larvae, all preferred food items of coastal fish (Zander and Hartwig, 1982; Antholz et al., 1991; Zander et al., 2015). Therefore, high abundance of filamentous algal species in the coastal zone could even increase the abundance of available prey for fish. In contrast, the loss of *C. tenuicorne*, which hosted the highest abundance of epifauna of all the studied algal species, could result in decline in secondary production.

Nevertheless, the consequences of a possible loss of algal species are dependent on abundances of both the host algae and the epifauna. Therefore, in order to estimate the reef wide impacts of algal species loss, the distribution and abundance of the algal species in the area should be known. Furthermore, the ephemeral algae are the most variable part of the macroalgal vegetation in the Baltic Sea as they can grow fast but live only a short period. The dominant species may also change between years (Kiirikki and Lehvo, 1997) making it even harder to estimate the abundance of different algae and thereby the consequences of algal species loss. The impacts on the higher trophic levels are also affected by which algal species will be lost and which algal species, if any, will occupy the place of the lost alga. Furthermore, the disturbance leading to loss of an algal species (such as excessive sedimentation) may even directly have a negative impact on the distribution of some epifauna such as *M. trossulus* (Kiirikki and Lehvo, 1997; Westerborn et al., 2008). On the other hand, for mobile epifauna, that have a possibility to flee, the impacts may not be as harsh (Kuno, 1981; Davenport et al., 1999). Indeed, it should not be forgotten that in these complex environments several factors may play a role in affecting the distribution of epifauna in the algae. In addition to diurnal variation (Buschmann, 1990) and seasonal variation (Johnson and Scheibling, 1987; Parker et al., 2001; Norderhaug et al., 2012), migration to more favorable conditions may take place as a result of e.g. occasional oxygen depletion (Kolar and Rahel, 1993) or during low tides (Davenport et al., 1999). It has been suggested that juvenile *Idotea* spp., utilize *C. glomerata* in the beginning of the summer and when *C. glomerata* starts to detach, they move to *F. vesiculosus* stands (Salemaa, 1979), highlighting the importance of perennial algal species for epifaunal taxa with a longer life span. The epifauna are also likely to be body size dependent when choosing a habitat (Hacker and Steneck, 1990) and therefore *F. vesiculosus* and *F. lumbricalis* may provide more important habitats for the adult epifaunal individuals, whereas the filamentous algal species are preferred by the juveniles. Also, *F. vesiculosus* and *F. lumbricalis* are known for their importance for fish as spawning and nursery grounds (Jansson et al., 1982; Kautsky

et al., 1992; Šaškov et al., 2014) and the consequences of losing them could therefore be severe for the coastal fish populations. Furthermore, a decline of *F. vesiculosus* may also result in loss of obligate epiphytic algal species such as *Elachista fucicola* (Velley, Areschoug, 1842) (Wikström and Kautsky, 2007).

In order to fully understand and predict the effects of algal species decline and loss in the changing environment, the distribution and abundance of different algal species in the area should be well known. Also, studies on how the algae associated epifauna utilize different algal species in different temporal scales are needed as well as further investigations of the functions macroalgal species provide for epifauna and fish.

4.4. Methodology

The quantitative sampling and comparison of the epifaunal taxa in separate algal species is not an easy task as the algal species differ in size, form and abundance. Epifaunal abundance and diversity can even differ vertically between different parts of a single alga such as in the Cladophora-belt (Jansson, 1967) or in kelps (Christie et al., 2007). Nevertheless, the surface area of an algae and the area between the algal structures are probably important for quantifying its epifaunal assemblages (Warfe et al., 2008) as also indicated by our results. One method for quantifying the surface area is to scan pressed macrophyte samples and measure the perimeter of the shoots and two-dimensional surface with computer software as done by Hansen et al. (2011). However, this is rather challenging to perform for fine filamentous algae. A widely used method for collecting macroalgae is to use a frame of standardized size (Råberg and Kautsky, 2007; Wikström and Kautsky, 2007; Christie et al., 2009) where everything that grows inside the frame is scraped off and used as a sample. This is not always optimal because algal species are seldom found in monocultures and therefore such large samples will likely include more than one algal species and also fauna attached to the bottom and not necessarily living on the sampled algae. Further, successful sampling of monocultures of different algal species from the same depths with the same exposure is challenging if not impossible.

Our sampling technique was easy and precise to use since only the targeted algal species of appropriate size were collected. This made it possible to take a large number of samples without ending up with too many months of sorting the algal epifauna in the laboratory. The samples were also collected from the same sampling sites with comparable exposure, depth and water quality to reduce the small scale spatial effects. But, our samples were not standardized for a specific surface area and therefore the discussion on the reef wide impacts of changing algal communities is limited. Finding cost efficient methods for sampling and quantifying the epifaunal composition in macroalgae is important for developing standardized monitoring methods and indicators for following environmental changes in the shallow rocky shores required by EU's marine Strategy Framework Directive (European commission, 2008). As epifauna both affect and are affected by macroalgae and fish, they may provide a good indicator for detecting changes in

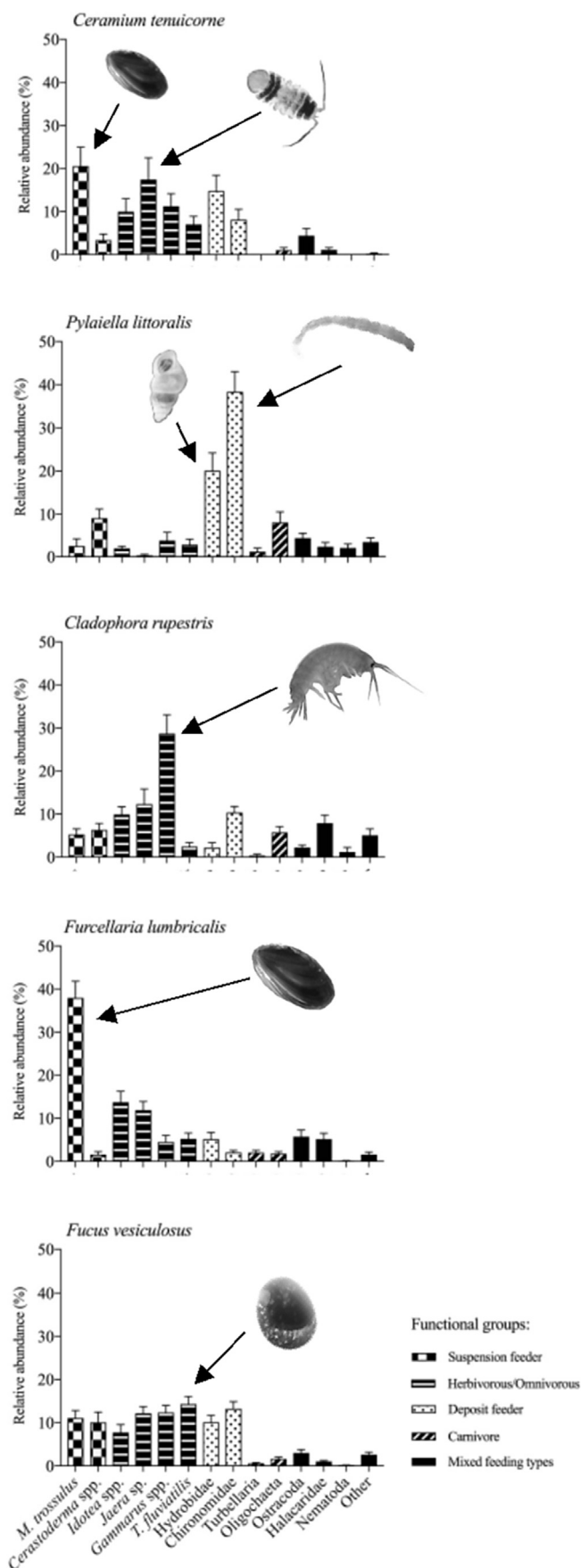


Fig. 4. Relative epifaunal abundances in % (mean and SE) of the most abundant epifaunal taxa from all the studied macroalgal species. The pattern of the bars indicates the functional groups of the epifauna.

both algal composition as well as in fish communities. This requires though that standardized sampling methods are developed and agreed upon.

5. Conclusions

Our results indicate that changes in algal species composition will affect dominance patterns in epifaunal communities in the coastal zone and further ecosystem functions and energy flows to the higher trophic levels. We found that the epifaunal composition differs among the studied algal species but that only few if any epifaunal species seem to be dependent on any single algal species. This suggests that if a few algal species were lost from the ecosystem, other algal species could compensate partially for the loss of these as habitats for the epifauna as suggested earlier by Bates and DeWreede (2007).

The epifauna diversity, but not abundance, was highest in canopy forming and filamentous perennial algal species and the sampling method was found to be precise and effective for studies on hard bottom invertebrate communities.

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References

- Antholz, B., Meyer-Antholz, W., Zander, C.D., 1991. Feeding activities of two euryhaline small-sized fish in a western Baltic brackish fjord. *Helgol. Meeresunters.* 45 (3), 287–300. <http://dx.doi.org/10.1007/BF02365521>.
- Bates, C.R., 2009. Host taxonomic relatedness and functional-group affiliation as predictors of seaweed–invertebrate epifaunal associations. *Mar. Ecol. Prog. Ser.* 387, 125–136. <http://dx.doi.org/10.3354/meps08089>.
- Bates, C.R., DeWreede, R.E., 2007. Do changes in seaweed biodiversity influence associated invertebrate epifauna? *J. Exp. Mar. Biol. Ecol.* 344 (2), 206–214. <http://dx.doi.org/10.1016/j.jembe.2007.01.002>.
- Bayne, B.L., 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *J. Animal Ecol.* 33, 513–523.
- Brennan, A., McLachlan, A.J., 1979. Tubes and tube-building in a lotic chironomid (Diptera) community. *Hydrobiologia* 67 (2), 173–178.
- Brönmark, C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* 45, 26–30.
- Bucas, M., 2009. Distribution Patterns and Ecological Role of the Red Alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux off the Exposed Baltic Sea Coast of Lithuania. Doctoral degree theses of Ph. D. in ecology and environmental studies. Klaipėda University, Klaipėda. <http://dx.doi.org/10.1515/BOT.2006.037>.
- Buschmann, A.H., Bravo, A., 1990. Intertidal amphipods as potential dispersal agents of carpospores of *Iridaea laminarioides* (gigartinales, rhodophyta). *J. Phycol.* 26 (3), 417–420.
- Buschmann, A.H., 1990. Intertidal macroalgae as refuge and food for Amphipoda in central Chile. *Aquat. Bot.* 36 (3), 237–245.
- Bäck, S., Ruuskanen, A., 2000. Distribution and maximum growth depth of *Fucus vesiculosus* along the Gulf of Finland. *Mar. Biol.* 136 (2), 303–307. <http://dx.doi.org/10.1007/s002270050688>.
- Christie, H., Jørgensen, N.M., Norderhaug, K.M., 2007. Bushy or smooth, high or low; importance of habitat architecture and vertical position for distribution of fauna on kelp. *J. Sea Res.* 58 (3), 198–208. <http://dx.doi.org/10.1016/j.seares.2007.03.006>.
- Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. *Mar. Ecol. Prog. Ser.* 396, 221–233. <http://dx.doi.org/10.3354/meps08351>.
- Costanza, R., d'Arge, R., De Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sluttkopf, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260. <http://dx.doi.org/10.1038/387253a0>.
- Crowe, T.P., Thompson, R.C., Bray, S., Hawkins, S.J., 2000. Impacts of anthropogenic

- stress on rocky intertidal communities. *J. Aquatic Ecosyst. Stress Recovery* 7 (4), 273–297. <http://dx.doi.org/10.1023/A:1009911928100>.
- Davenport, J., Butler, A., Cheshire, A., 1999. Epifaunal composition and fractal dimensions of marine plants in relation to emersion. *J. Mar. Biol. Assoc. U. K.* 79 (02), 351–355.
- Duplisea, D.E., 2000. Benthic organism biomass size-spectra in the Baltic Sea in relation to the sediment environment. *Limnol. Oceanogr.* 45, 558–568. <http://dx.doi.org/10.4319/lo.2000.45.3.0558>.
- Eriksson, B.K., Johansson, G., Snoeijs, P., 1998. Long-term changes in the sublittoral zonation of brown algae in the southern Bothnian Sea. *Eur. J. Phycol.* 33 (3), 241–249. <http://dx.doi.org/10.1080/09670269810001736743>.
- Eriksson, B.K., Ljunggren, L., Sandström, A., Johansson, G., Mattila, J., Rubach, A., Råberg, S., Snickars, M., 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecol. Appl.* 19 (8), 1975–1988.
- Eriksson Wiklund, A.K., Malm, T., Honkakangas, J., Eklund, B., 2012. Spring development of hydrolittoral rock shore communities on wave-exposed and sheltered sites in the northern Baltic proper. *Oceanologia* 54 (1), 75–107. <http://dx.doi.org/10.5697/oc.54-1.075>.
- European commission, 2008. Marine strategy Framework directive. *Eur. Communities Official J.* L164, 19–40.
- Fenwick, G.D., 1976. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownii*. *J. Exp. Mar. Biol. Ecol.* 25 (1), 1–18.
- Grzelak, K., Kuklinski, P., 2010. Benthic assemblages associated with rocks in a brackish environment of the southern Baltic Sea. *J. Mar. Biol. Assoc. U. K.* 90 (01), 115–124.
- Hacker, S.D., Madin, L.P., 1991. Why habitat architecture and color are important to shrimps living in pelagic Sargassum: use of camouflage and plant-part mimicry. *Mar. Ecol. Prog. Ser.* 70 (2), 143–155. <http://dx.doi.org/10.3354/meps070143>.
- Hacker, S.D., Steneck, R.S., 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71 (6), 2269–2285.
- Hansen, J.P., Wikström, S.A., Axemar, H., Kautsky, L., 2011. Distribution differences and active habitat choices of invertebrates between macrophytes of different morphological complexity. *Aquat. Ecol.* 45 (1), 11–22. <http://dx.doi.org/10.1007/s10452-010-9319-7>.
- Harley, C.D., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., Graham, M.H., 2012. Effects of climate change on global seaweed communities. *J. Phycol.* 48 (5), 1064–1078. <http://dx.doi.org/10.1111/j.1529-8817.2012.01224.x>.
- Himmelman, J.H., Steele, D.H., 1971. Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Mar. Biol.* 9 (4), 315–322. <http://dx.doi.org/10.1007/BF00372825>.
- Holmlund, M.B., Peterson, C.H., Hay, M.E., 1990. Does algal morphology affect amphipod susceptibility to fish predation? *J. Exp. Mar. Biol. Ecol.* 139 (1–2), 65–83. [http://dx.doi.org/10.1016/0022-0981\(90\)90039-F](http://dx.doi.org/10.1016/0022-0981(90)90039-F).
- Isæus, M., 2004. Factors Structuring *Fucus* Communities at Open and Complex Coastlines in the Baltic Sea. Doctoral thesis. Department of Botany, Stockholm University.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.V., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638. <http://dx.doi.org/10.1126/science.1059199>.
- Jansson, A.M., 1967. The food-web of the *Cladophora*-belt fauna. *Helgoländer Wiss. Meeresunters.* 15, 574–588. <http://dx.doi.org/10.1007/BF01618652>.
- Jansson, A.M., Kautsky, N., von Oertzen, J.A., Schramm, W., Sjöstedt, B., von Wachenfeldt, T., Wallentinus, I., 1982. Structural and Functional Relationships in a Southern Baltic *Fucus* Ecosystem. Originally Published in Contributions from the Askö Laboratory. University of Stockholm, Sweden.
- Johnson, S.C., Scheibling, R.E., 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 209–227.
- Jormalainen, V., Gagnon, K., Sjöroos, J., Rothäusler, E., 2016. The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biol. Invasions* 18 (5), 1409–1419. <http://dx.doi.org/10.1007/s10530-016-1090-9>.
- Jormalainen, V., Honkanen, T., Heikkilä, N., 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar. Ecol. Prog. Ser.* 220, 219–230. <http://dx.doi.org/10.3354/meps220219>.
- Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L., Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecol. Evol.* 3 (5), 1356–1373. <http://dx.doi.org/10.1002/ece3.541>.
- Jutterström, S., Andersson, H.C., Omstedt, A., Malmaeus, J.M., 2014. Multiple stressors threatening the future of the Baltic Sea—Kattegat marine ecosystem: implications for policy and management actions. *Mar. Pollut. Bull.* 86 (1), 468–480. <http://dx.doi.org/10.1016/j.marpolbul.2014.06.027>.
- Jørgensen, N.M., Christie, H., 2003. Diurnal, horizontal and vertical dispersal of kelp-associated fauna. *Hydrobiologia* 503 (1–3), 69–76. <http://dx.doi.org/10.1023/B:HYDR.0000008491.89382.e5>.
- Kangas, P., Autio, H., Hällfors, G., Luther, H., Niemi, Å., Salemaa, H., 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. *Acta Bot. Fenn.* 118, 1–27.
- Karez, R., Engelbert, S., Sommer, U., 2000. Co-consumption and protective coating: two new proposed effects of epiphytes on their macroalgal hosts in mesograzers-epiphyte-host interactions. *Mar. Ecol. Prog. Ser.* 205, 85–93.
- Kautsky, H., Martin, G., Mäkinen, A., Borgiel, M., Vahteri, P., Rissanen, J., 1999. Structure of phytobenthic and associated animal communities in the Gulf of Riga. *Hydrobiologia* 393, 191–200. <http://dx.doi.org/10.1023/A:1003510105274>.
- Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U., Lindblad, C., 1992. Studies on the *Fucus vesiculosus* community in the Baltic sea. *Acta Phytogeogr. Suec.* 78, 33–48.
- Kautsky, N., Kautsky, H., Kautsky, U., Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940's indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28 (1), 1–8. <http://dx.doi.org/10.3354/meps028001>.
- Keith, D.E., 1971. Substrate selection in caprellid amphipods of southern California, with emphasis on *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda). *Pac. Sci.* 25, 387–394. <http://dx.doi.org/10.1163/156854069X00367>.
- Kiirikki, M., Lehto, A., 1997. Life strategies of filamentous algae in the northern Baltic Proper. *Sarsia* 82 (3), 259–267. <http://dx.doi.org/10.1080/00364827.1997.10413653>.
- Kolar, C.S., Rahel, F.J., 1993. Interaction of a biotic factor (predator presence) and an abiotic factor (low oxygen) as an influence on benthic invertebrate communities. *Oecologia* 95 (2), 210–219. <http://dx.doi.org/10.1007/BF00323492>.
- Kotta, J., Paalme, T., Martin, G., Mäkinen, A., 2000. Major changes in macroalgal community composition affect the food and habitat preference of *Idotea baltica*. *Int. Rev. Hydrobiol.* 85, 697–705. [http://dx.doi.org/10.1002/1522-2632\(200011\)85:5/6<697::AID-IROH697>3.0.CO;2-0](http://dx.doi.org/10.1002/1522-2632(200011)85:5/6<697::AID-IROH697>3.0.CO;2-0).
- Kraufvelin, P., Salovius, S., 2004. Animal diversity in Baltic rocky shore macroalgae: can *Cladophora glomerata* compensate for lost *Fucus vesiculosus*? *Estuar. Coast. Shelf Sci.* 61 (2), 369–378. <http://dx.doi.org/10.1016/j.ecss.2004.06.006>.
- Krause-Jensen, D., Carstensen, J., Dahl, K., Bäck, S., Neuvonen, S., 2009. Testing relationships between macroalgal cover and Secchi depth in the Baltic Sea. *Ecol. Indic.* 9 (6), 1284–1287. <http://dx.doi.org/10.1016/j.ecolind.2009.02.010>.
- Kuno, E., 1981. Dispersal and the persistence of populations in unstable habitats: a theoretical note. *Oecologia* 49, 123–126.
- Lippert, H., Iken, K., Rachor, E., Wiencke, C., 2001. Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). *Polar Biol.* 24 (7), 512–522. <http://dx.doi.org/10.1007/s003000100250>.
- Little, C., Williams, G.A., Trowbridge, C.D., 2009. *The Biology of Rocky Shores*, second ed. Oxford University Press, p. 356.
- Littler, M.M., Murray, S.N., 1974. The primary productivity of marine macrophytes from a rocky intertidal community. *Mar. Biol.* 27 (2), 131–135.
- MacNeil, C., Dick, J.T., Elwood, R.W., 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biol. Rev.* 74 (4), 375–395. <http://dx.doi.org/10.1111/j.1469-185X.1999.tb00035.x>.
- Mann, K.H., 1973. Seaweeds: their productivity and strategy for growth. *Science* 182 (4116), 975–981. <http://dx.doi.org/10.1126/science.177.4047.410>.
- Martin-Smith, K.M., 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *J. Exp. Mar. Biol. Ecol.* 174 (2), 243–260.
- Morse, D.R., Lawton, J.H., Dodson, M.M., Williamson, M.H., 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314, 731–733.
- Norderhaug, K.M., Christie, H., 2011. Secondary production in a *Laminaria hyperborea* kelp forest and variation according to wave exposure. *Estuar. Coast. Shelf Sci.* 95 (1), 135–144. <http://dx.doi.org/10.1016/j.ecss.2011.08.028>.
- Norderhaug, K.M., Christie, H., Fosså, J.H., Fredriksen, S., 2005. Fish—macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. *J. Mar. Biol. Assoc. U. K.* 85 (05), 1279–1286. <http://dx.doi.org/10.1017/S0025315405012439>.
- Norderhaug, K.M., Christie, H., Andersen, G.S., Bekkby, T., 2012. Does the diversity of kelp forest macrofauna increase with wave exposure? *J. Sea Res.* 69, 36–42. <http://dx.doi.org/10.1016/j.seares.2012.01.004>.
- Norderhaug, K.M., Christie, H.C., Rinde, E., Gundersen, H., Bekkby, T., 2014. Importance of wave and current exposure to fauna communities in *Laminaria hyperborea* kelp forest. *Mar. Ecol. Prog. Ser.* 502, 295–301. <http://dx.doi.org/10.3354/meps10754>.
- Norderhaug, K.M., Fredriksen, S., Nygaard, K., 2003. Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar. Ecol. Prog. Ser.* 255, 135–144. <http://dx.doi.org/10.3354/meps255135>.
- Nummelin, C., 2000. Vattenmiljön i Kring Åland – Miljöstillståndsrapport, 1999. Mariehamn: Mariehamns tryckeri. (in Swedish).
- Orav-Kotta, H., Kotta, J., 2003. Seasonal variations in the grazing of *Gammarus oceanicus*, *Idotea baltica*, and *Palaemon adspersus*. In: *Proceedings of the Estonian Academy of Sciences, Biology and Ecology*, vol. 52. Estonian Academy Publishers, pp. 141–148 (2).
- Orav-Kotta, H., Kotta, J., Herkül, K., Kotta, I., Paalme, T., 2009. Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* (Amphipoda: Crustacea) in the northern Baltic Sea. *Biol. Invasions* 11 (3), 597–608. <http://dx.doi.org/10.1007/s10530-008-9274-6>.
- Parker, J.D., Duffy, J.E., Orth, R.J., 2001. Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Mar. Ecol. Prog. Ser.* 224, 55–67. <http://dx.doi.org/10.3354/meps224055>.
- Philippart, C.J., Anadón, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F., Hawkins, S.J., Oguz, T., O'Sullivan, G., Reid, P.C., 2011. Impacts of climate change on European marine ecosystems: observations, expectations and indicators. *J. Exp. Mar. Biol. Ecol.* 400 (1), 52–69. <http://dx.doi.org/10.1016/j.jembe.2011.02.023>.
- Pihl, L., Isaksson, I., Wennhage, H., Moksnes, P.O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of

- epibenthic fauna and fish. *Netherl. J. Aquatic Ecol.* 29 (3–4), 349–358.
- Poore, A.G., 2004. Spatial associations among algae affect host use in a herbivorous marine amphipod. *Oecologia* 140 (1), 104–112. <http://dx.doi.org/10.1111/j.1558-5646.2007.00261.x>.
- Prathey, A., Marrs, R., Norton, T., 2003. Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. *Mar. Biol.* 142 (2), 381–390. <http://dx.doi.org/10.1007/s00227-002-0940-4>.
- Ryther, J.H., 1963. Geographic variations in productivity. In: Hill, M.N. (Ed.), *The Sea*. John Wiley Sons, New York, pp. 347–380.
- Råberg, S., Kautsky, L., 2007. A comparative biodiversity study of the associated fauna of perennial furoids and filamentous algae. *Estuar. Coast. Shelf Sci.* 73 (1), 249–258. <http://dx.doi.org/10.1016/j.ecss.2007.01.005>.
- Rönnberg, O., Lehto, J., Haahtela, I., 1985. Recent Changes in the Occurrence of *Fucus Vesiculosus* in the Archipelago Sea, SW Finland. *Annales Botanici Fennici. The Finnish Botanical Publishing Board*, pp. 231–244.
- Rönnbäck, P., Kautsky, N., Pihl, L., Troell, M., Söderqvist, T., Wennhage, H., 2007. Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. *AMBIO a J. Hum. Environ.* 36 (7), 534–544. [http://dx.doi.org/10.1579/0044-7447\(2007\)36\[534:EGASFS\]2.0.CO;2](http://dx.doi.org/10.1579/0044-7447(2007)36[534:EGASFS]2.0.CO;2).
- Salemaa, H., 1979. Ecology of *Idotea* spp. (Isopoda) in the northern baltic. *Ophelia* 18 (1), 133–150.
- Salovius, S., Kraufvelin, P., 2004. The filamentous green alga *Cladophora glomerata* as a habitat for littoral macro-fauna in the northern Baltic Sea. *Ophelia* 58 (2), 65–78. <http://dx.doi.org/10.1080/00785326.2004.10410214>.
- Šaškov, A., Šiaulys, A., Bučas, M., Daunys, D., 2014. Baltic herring (*Clupea harengus membras*) spawning grounds on the Lithuanian coast: current status and shaping factors. *Oceanologia* 56 (4), 789–804. <http://dx.doi.org/10.5697/oc.56-4.789>.
- Schramm, W., Nienhuis, P. (Eds.), 1996. *Marine benthic Vegetation: Recent Changes and the Effects of Eutrophication* (No. 123). Springer Science Business Media.
- Seed, R., Elliott, M., Boaden, P.J.S., O'Connor, R., 1981. The composition and seasonal changes amongst the epifauna associated with *Fucus serratus* L. in Strangford Lough, Northern Ireland. *Cah. Biol. Mar.* 3, 243–266.
- Seed, R., O'Connor, R.J., 1981. Community organization in marine algal epifaunas. *Annu. Rev. Ecol. Syst.* 12, 49–74.
- Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68 (3), 299–319.
- Svensson, P.A., Malm, T., Engkvist, R., 2004. Distribution and host plant preference of *Idotea baltica* (Pallas) (Crustacea: Isopoda) on shallow rocky shores in the central Baltic Sea. *Sarsia* 89 (1), 1–7. <http://dx.doi.org/10.1080/00364820310003217>.
- Svensson, F., 2015. Effects of Warming on the Ecology of Algal-dominated Phyto-benthic Communities in the Baltic Sea. Doctoral thesis. Stockholm University, Faculty of Science, Department of Ecology, Environment and Plant Sciences.
- Taylor, R.B., Cole, R.G., 1994. Mobile epifauna on subtidal brown sea-weeds in northeastern New Zealand. *Mar. Ecol. Prog. Ser.* 115 <http://dx.doi.org/10.3354/meps115271>, 271–271.
- Veber, T., Kotta, J., Lauringson, V., Kotta, I., 2009. Influence of the local abiotic environment, weather and regional nutrient loading on macrobenthic invertebrate feeding groups in a shallow brackish water ecosystem. *Oceanologia* 51 (4), 541–559.
- Waern, M., 1952. Rocky-shore algae in the Öregrund archipelago. *Acta Phytogeogr. Suec.* 30, 1–298.
- Wallin, A., Qvarfordt, S., Norling, P., Kautsky, H., 2011. Benthic communities in relation to wave exposure and spatial positions on sublittoral boulders in the Baltic Sea. *Aquat. Biol.* 12 (2), 119–128. <http://dx.doi.org/10.3354/ab00329>.
- Warfe, D.M., Barmuta, L.A., Wotherspoon, S., 2008. Quantifying habitat structure: surface convolution and living space for species in complex environments. *Oikos* 117 (12), 1764–1773. <http://dx.doi.org/10.1111/j.1600-0706.2008.16836.x>.
- Wernberg, T., Thomsen, M.S., Kotta, J., 2013. Complex plant–herbivore–predator interactions in a brackish water seaweed habitat. *J. Exp. Mar. Biol. Ecol.* 449, 51–56. <http://dx.doi.org/10.1016/j.jembe.2013.08.014>.
- Westerbom, M., Mustonen, O., Kilpi, M., 2008. Distribution of a marginal population of *Mytilus edulis*: responses to biotic and abiotic processes at different spatial scales. *Mar. Biol.* 153 (6), 1153–1164. <http://dx.doi.org/10.1007/s00227-007-0886-7>.
- Wikström, S.A., Kautsky, L., 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuar. Coast. Shelf Sci.* 72 (1), 168–176. <http://dx.doi.org/10.1016/j.ecss.2006.10.009>.
- Zander, C.D., Hartwig, E., 1982. On the biology and food of small-sized fish from North and Baltic Sea areas. IV. Investigations on an eulittoral mud flat at Sylt Island. *Helgoländer Meeresunters.* 35 (1), 47–63. <http://dx.doi.org/10.1007/BF02289834>.
- Zander, C.D., Rupp, K., Böhme, K., Brix, S., Detloff, K.C., Melander, J., Nordhaus, I., Schiro, C., 2015. The phytal fauna of the SW Baltic Sea and its importance as reservoir for fish prey. *Bull. Fish Biol.* 15 (1/2), 33–51.